

Niche change analysis as a tool to inform management of two invasive species in Eastern Africa

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Abstract. Significant progress has been made in providing guidelines and recommendations for assessing the ecological niche, stage of invasion, and probability of invasive alien plant species (IAPS) potential distribution in space and time. We followed these recommendations by developing and comparing ordination and species distribution models (SDMs) of two important woody IAPS in Eastern Africa, *Prosopis juliflora* and *Lantana camara*, and interpreting the results to inform IAPS management. The two species differ in their invasion history in Eastern Africa; while *L. camara* was widely introduced there in the 19th century, *P. juliflora* was only planted at selected locations in the 1970s and 1980s. For the SDMs, machine learning algorithms were used to generate one ensemble model each for *P. juliflora* and *L. camara*. For ordination, we used bioclimatic variables, performed a principal component analysis, and compared the native and global niches of the species with the Eastern African niche. Niches varied substantially depending on the percentage of marginal climates excluded from the models. Additional analysis of the local niches surrounding the original *P. juliflora* plantations showed that they are complementary, which may have led to an overestimation of regional niche filling. While niche expansion was absent or small depending on the percentage of marginal climates excluded, analysis of the stages of invasion suggested that *P. juliflora* may have started to adapt to novel climatic conditions and that *L. camara* is approaching a pseudo-stable equilibrium in Eastern Africa. The SDMs showed that large areas in Eastern Africa that have not yet been invaded by *P. juliflora* are suitable or will become suitable with climate change. For *L. camara*, the global SDM predicted a considerably larger suitable area than the Eastern African one, raising uncertainty about the areas to be included in a regional management strategy. Thus, combining ordination and SDMs and integrating a geographic component into ordination is useful in assessing IAPS invasion stages and potential niche shifts, and the results help inform IAPS policy and management. The combined approach can also serve to guide experimental studies addressing divergences between results generated with the different approaches.

Key words: biological invasions; Eastern Africa; ecological niche; invasion stage; *Lantana camara*; *Prosopis juliflora*; species distribution modeling.

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INTRODUCTION

Invasive alien plant species (IAPS) are considered to have serious impacts on ecosystem functioning, the supply of ecosystem services, and human well-being (Vilà et al. 2011, Simberloff et al. 2013, Vilà and Hulme 2017). In response to the threat they pose, a number of international agreements have been developed that urge member states to prevent the introduction and spread of IAPS (Shine et al. 2000). Once an IAPS has established itself widely in its introduced range, complete eradication is no longer feasible (Parkes and Panetta 2009). Rather, it should be managed according to a spatially explicit management strategy that sets different control objectives for areas with different invasion levels (Grice et al. 2011, Terblanche et al. 2016, Shackleton et al. 2017b). Developing such a strategy requires a holistic understanding of a species' stage of invasion and the invasion process, including factors affecting its local abundance, spread, and impact. Furthermore, to develop a spatially explicit management strategy, it is essential to assess (1) the current and projected future geographic distribution and abundance of the target IAPS, and (2) its ecological niche in the invaded range in comparison with the global or native niche under current and projected climates.

A range of modeling approaches have been developed to compare IAPS' ecological niches and understand their current stages of invasion, as well as to project species' potential distribution in space and/or time (Guisan and Thuiller 2005, Elith and Leathwick 2009). They can be grouped into two modeling types: mechanistic models and statistical, correlative models (Kearney and Porter 2009). Mechanistic models incorporate functional traits of species and thus require collection and validation of a large amount of physiological data, whereas statistical, correlative models rely on a set of geographic species occurrence and preexisting environmental data. Within statistical, correlative modeling, two techniques can be differentiated: ordination, which is based on direct observations, and species distribution modeling (also known as

ecological niche modeling), which is based on predictions. They both rely on the ecological niche concept and may be considered complementary. While ordination provides insights into changes in macroclimate niches, species distribution model (SDM) predictions in geographic space identify regions that might be at risk of being invaded (Guisan et al. 2014). Both approaches use observed occurrences and relate biotic and abiotic conditions to the probability of a species being present at a specific location. Usually it is assumed that the species' ecological niche is stable in space and time and that the species has filled it and is in quasi-equilibrium with its regional environment. In the case of IAPS, both assumptions are often wrong (Gallien et al. 2012). In fact, the realized regional niches of an IAPS may differ significantly between its native and invaded ranges (Guisan et al. 2014). Three different situations of niche occupation may occur in the invaded range: The invasive species occupies (1) a part of its global niche (e.g., due to local biotic limitations) that is similar to the realized niche in its native range; (2) a part of its global niche that is different from the realized niche in its native range; or (3) areas both inside and outside its global niche, as a result of rapid genetic adaptation to the novel environmental conditions in the invaded range (Gallien et al. 2010, 2014).

A large number of woody plant species worldwide were deliberately introduced to areas outside their native range during the 19th and 20th centuries, mainly for amenity, forestry, or agricultural purposes (Binggeli 1996). To date, woody IAPS are overproportionally represented among the alien plant species causing impacts on resident communities (Pyšek et al. 2012), posing significant threats to the provisioning of ecosystem services and rural livelihoods (Pejchar and Mooney 2009, Vilà and Hulme 2017). Among the most frequently mentioned IAPS causing severe environmental and socioeconomic problems in Africa and elsewhere are *Prosopis* spp.—particularly *Prosopis juliflora* (Sw.) DC.—and *Lantana camara* L. (Henderson 2007, Boy and Witt 2013). Both species can alter ecosystem processes and

are hence considered ecosystem engineers (Richardson and Van Wilgen 2004). In Eastern Africa, they affect open and semi-open ecosystems such as grasslands and savannahs and cause significant problems in cropping systems (Witt and Luke 2017). While both *P. juliflora* and *L. camara* are among the world's 100 worst invasive species (Lowe et al. 2000), they differ considerably in their ecological niches and their invasion histories, and hence also in their current distribution. *L. camara* was widely introduced to Eastern Africa already in the first half of the 19th century. In contrast, *P. juliflora* was planted at selected locations in Eastern Africa only in the 1970s, and most of the original plantations are still present. The two species' different invasion histories may have potentially significant implications regarding their current realized ecological niches, evidence of niche shifts in the invaded range, and the risk of future invasion of new geographic areas in Eastern Africa.

The purpose of this study was to perform a comprehensive assessment of the specific regional niches, suitable habitats, and potential spread of *P. juliflora* and *L. camara* in Ethiopia, Kenya, and Tanzania that can serve as a baseline for the formulation of recommendations with regard to prevention measures to support effective regional and national IAPS management strategies in Eastern Africa. We applied the frameworks and followed the guidance of Guisan et al. (2014) and Gallien et al. (2012), combining ordination and SDM, which has been rarely done so far (Guisan et al. 2014). This enabled us to compare the two species' global, native, and Eastern African niches, assess their current stages of invasion, and reveal their invasion pattern. In addition, we assessed the two species' potential future geographic distributions in Eastern Africa under a changing climate. Based on our findings, we give recommendations for effective management of the two IAPS in Eastern Africa, with a view to preventing further spreading of the species and reducing their negative impacts on Eastern African countries' ecosystems and economies.

MATERIALS AND METHODS

Target species

This study focuses on two woody IAPS in Ethiopia, Kenya, and Tanzania: *P. juliflora* (Sw.)

DC. and *L. camara* L. The evergreen *P. juliflora*, which belongs to the Mimosaceae family and is native to Central and South America (Pasiecznik et al. 2001), is a nitrogen-fixing and salt- as well as drought-tolerant leguminous shrub or tree with an extensive and deep root system. It produces palatable pods and can form dense, impenetrable thorn forests (Robinson et al. 2010). The first introductions of *P. juliflora* and other South American representatives of the genus *Prosopis* to Eastern Africa took place during the 1970s and 1980s. In Ethiopia, *P. juliflora* was first introduced and planted in the late 1970s in a nursery in West Hararghe; in the early 1980s, the trees were transferred to the Afdem and Afar regions (Kebede and Coppock 2015). In Kenya, *P. juliflora* was planted widely as part of dryland reforestation programs in the 1980s, for example, in Bura on Tana River and in Baringo and Turkana counties (Harris et al. 2006). The aims were to prevent desertification, produce fuelwood to relieve the high pressure on native tree species, and provide an alternative source of livestock feed (Kariuki 1993, Lenachuru 2003). Difficulties arose soon after, in the early 1990s, when the tree began to invade cropland, grassland, riverbanks, and roadsides, thereby causing significant environmental problems and costs (Shackleton et al. 2014, Shiferaw et al. 2019). Today, *P. juliflora* is a declared noxious weed in several African countries, notably Kenya, Ethiopia, and Sudan (CABI 2015). In Ethiopia, it has invaded such large areas of former grazing land that this has led to conflicts among pastoralist groups (Kebede and Coppock 2015). While most invasive *Prosopis* trees in South Africa are hybrids (Mazibuko 2012), recent genetic studies corroborate earlier findings that almost all invasive *Prosopis* trees in Eastern Africa are indeed *P. juliflora* (M. L. Castillo 2018, public communications).

Lantana camara is a highly variable species belonging to the Verbenaceae family. Hundreds of cultivars and hybrids exist (Howard 1969). It is a multi-stemmed, medium-sized woody shrub which is native to Central and South America (Sundaram and Hiremath 2012). The species is poorly investigated in its native range, the extent of which is unclear. *L. camara* is able to invade most habitats from sea level to about 1800 m, except arid areas (Thomas and Ellison 2000). It is likely that its invasion history and its adaptive

evolution—due to its ability to hybridize—favor niche shifts (Sanders 2006). *L. camara* was introduced to Eastern Africa in the 19th century as an ornamental plant (Day et al. 2003, Sharma et al. 2005). It invades cropland and grassland, thereby reducing accessibility (Van Wilgen et al. 2008) and fodder production (Kohli et al. 2006). It has been shown to have negative impacts on biodiversity and native tree regeneration (Gooden et al. 2009). It increases the risk of fire, is poisonous to livestock if eaten in large amounts (Sharma et al. 1988), and acts a host for diseases and pests (CABI 2015).

Species data

To model the native and the global niches, we used data from the Global Biodiversity Information Facility (GBIF). We considered species occurrence (i.e., presence) data from the species' native ranges (Mexico, Central America) and from regions in the world where they have established themselves or become invasive (e.g., in Asia, Australia, South America, India, and Southern and Western Africa, and on the Arabian Peninsula), excluding points from Eastern Africa (which represents the regional niche we analyzed in this study). We used only points whose geolocation was indicated to at least three decimal places (in geographic coordinates and decimal degrees), which corresponds to about 11 km. This resulted in 1891 presence points for *P. juliflora* and 16,041 presence points for *L. camara* for the global niche (see Appendix S1: Figs. S1–S4 for their geographic locations and details on the number of presence points used for the native niche).

The taxonomic status of both species bears some level of uncertainty. The genetic diversity of the weedy types of *L. camara* is considered high, due to horticultural improvement which included crossing with other *Lantana* species (Day and Zalucki 2009). *P. juliflora* can also hybridize with other *Prosopis* species (Pasiiecznik et al. 2001), although recent molecular studies revealed that genotypes invasive in Eastern Africa almost always belong to *P. juliflora* (M. L. Castillo et al., *unpublished manuscript*). While selecting presence points for the two species, we took care to include points for the native niche only from areas where the two species are indeed considered native (Pasiiecznik et al. 2001, Day

and Zalucki 2009). For the global model, however, we cannot rule out that our presence points have a higher taxonomic variability, which may have led to a certain overestimation of the global niche—and, as a result, to an underestimation of regional niche expansion. We account for potential taxonomic variability by excluding 5% of marginal climates when calculating the different niches for each species.

We generated two sets of pseudo-absence points by means of random sampling within a 100-km buffer area around all species occurrence data points. Randomly generated absence points located <10 km from a presence point were removed. This resulted in two sets of approximately 1300 pseudo-absence points each for *P. juliflora* and two sets of approximately 1150 pseudo-absence points each for *L. camara*.

To model the Eastern African niches, we used data collected during several ground surveys between 2008 and 2017 (Ng et al. 2016, 2017, Shackleton et al. 2017a, Witt et al. 2018, Shiferaw et al. 2019). Occurrence data points were spatially rarefied using a 5 km distance in order to reduce spatial autocorrelation and obtain a more unbiased sample. The data set for *P. juliflora* contained 892 points, and that for *L. camara* contained 858 points. Again, we generated two random sets of pseudo-absence points for each plant species. Points closer than 10 km to another point were removed. This resulted in two pseudo-absence data sets of about 850 data points each for *P. juliflora* and two pseudo-absence data sets of about 730 and 826 data points, respectively, for *L. camara*. These four pseudo-absence data sets were further improved using the global niche modeling outputs. To reduce the influence of false absences, we removed points that were located within areas where more than one of the global distribution models suggested a presence of the respective species (Barbet-Massin et al. 2012). All species data used in this study can be found in Data S1.

Spatial data

To model the global and native niches, we used the 19 available bioclimatic variables of WorldClim (version 2) at a spatial resolution of 30 s (Fick and Hijmans 2017). We reduced the number of variables by only selecting those with the lowest correlation averages and the most

counts of pairwise variable correlation values <0.6 for each of our species. This led to the selection of three to four precipitation-related variables and three to four temperature-related ones for each species, resulting in two sets of seven and eight bioclimatic variables, respectively, for *P. juliflora* and *L. camara* (Table 1). We did not include any other variables in our global models; as all data sets have a spatial resolution of 250 m, including all of them would have exceeded the computational capacity of our facilities.

To model the regional niches in Eastern Africa, we again reduced the number of bioclimatic variables, this time using the Eastern Africa presence points. In order to obtain a refined model for our study area, we added seven non-climatic variables that had previously been shown to influence the distribution of invasive species (Elith et al. 2011, Mbaabu et al. 2019, Shiferaw et al. 2019). We additionally included two MODIS 16-day NDVI products with a 250 m spatial

resolution (Didan 2015) that had the highest model importance when running preliminary variable importance tests using only MODIS 16-day NDVI products captured in 2014. The year 2014 was slightly too warm in Eastern Africa but an average year in terms of rainfall (WMO 2015). Additionally, we chose two topographic variables, slope and elevation derived from SRTM version 4.1 (Jarvis et al. 2008), as well as two surface water related variables, distance to rivers and distance to waterbodies, which we generated ourselves, and one anthropogenic variable, the Global Human Footprint Index (GHI) data set (WCS and CIESIN 2005). The spatial resolution of the data sets provided in raster format varied between 90 m (topographic data sets), 250 m (the MODIS NDVIs), and 1000 m (bioclimatic variables and GHI). We resampled them to a common spatial resolution of 250 m.

To model the distribution of the two invasive species considering future climate scenarios we

Table 1. Overview of variables used in the Global/Native SDM (regular) and Regional SDM (bold) as well as the niche comparison (bold).

Variables	Abbreviation	Species			
		<i>Prosopis juliflora</i>		<i>Lantana camara</i>	
		Global/Native	Regional	Global/Native	Regional
Annual mean diurnal temperature range	bio2	X	X	X	(X)
Isothermality	bio3		X	X	
Temperature seasonality	bio4				(X)
Maximum temperature of warmest month	bio5				X
Temperature annual range	bio7	X	X	X	(X)
Mean temperature of wettest quarter	bio8	X		X	
Mean temperature of driest quarter	bio9		X		
Mean temperature of warmest quarter	bio10	X		X	
Annual precipitation	bio12			X	X
Precipitation of driest month	bio14	X			X
Precipitation seasonality	bio15		X		
Precipitation of wettest quarter	bio16				(X)
Precipitation of driest quarter	bio17		X		
Precipitation of warmest quarter	bio18	X	X	X	X
Precipitation of coldest quarter	bio19	X	X	X	
Slope		Not used	X	Not used	
Elevation		Not used	X	Not used	X
Distance to waterways		Not used	X	Not used	
Distance to waterbodies		Not used	X	Not used	X
Human Footprint Index		Not used	X	Not used	X
MODIS NDVI (17 January 2014)		Not used		Not used	X
MODIS NDVI (23 April 2014)		Not used	X	Not used	
MODIS NDVI (13 August 2014)		Not used		Not used	X
MODIS NDVI (29 August 2014)		Not used	X	Not used	

Notes: SDM, species distribution model. Variables with an X in brackets were removed during fine-tuning of the models; this was only necessary for regional SDM of *L. camara*.

used projections of the bioclimatic variables for 2050 (average for 2041–2060). We used data from the Coupled Model Intercomparison Project, Phase 5 (CMIP5) at 30 s spatial resolution and chose the representative concentration pathways (RCPs; van Vuuren et al. 2011) 45 and 85 using the global climate model developed at the Max Planck Institute for Meteorology, also known under the abbreviation MPI-ESM-LR (Stevens et al. 2013). This model has shown to perform acceptably well compared to other scenario models for Eastern Africa and the Horn of Africa (McSweeney et al. 2015, Klein et al. 2016). The chosen model predicts a warmer and drier climate for the study area, with increasing temperature seasonality and decreasing rainfall seasonality. Hereafter, we abbreviate the two future climate scenarios considered in this study as mp45 and mp85. The mp45 scenario is more moderate and the mp85 scenario extreme.

Modeling approach

We chose four different algorithms for the SDM: (1) random forest regression (RF), (2) support vector machine, (3) boosted regression trees in combination with *gbm.step* for the fine-tuning of the algorithm (BRT), and (4) maximum entropy (Maxent). We evaluated the models using *k*-fold cross-validation and focused on the performance parameters area under the curve (AUC; Swets 1988) and true skill statistics (TSS; Allouche et al. 2006). We only considered models achieving a TSS value of at least 0.5 and an AUC of at least 0.8 for further analysis. This selection is based on previous studies having either a similar objective or recommending thresholds for these two performance parameters (Araújo et al. 2005, Gallien et al. 2012). The four different algorithms in combination with the two pseudo-absence data sets resulted in eight different models (i.e., continuous probabilities) for each species for the global, the native, and the regional niches. For the calculation of optimum thresholds for each model, we used the *optim.thresh* function available in the R package *SDMTools* (version 1.1-221; Van Der Wal et al. 2019). We considered the optimum threshold to be the value, or range of values, that maximizes the sum of sensitivity and specificity. The models that fulfilled our accuracy performance requirements were then used to generate an ensemble model for each

species and scale. The ensembles were generated by calculating mean probabilities and mean optimum thresholds. We considered this methodology suitable because there was little variation between the qualifying models and thresholds (Marmion et al. 2009, Stohlgren et al. 2010). In the global model prediction using future climate scenarios, we did not permit clamping as we aimed at obtaining conservative model predictions (Guisan et al. 2014). All model calculations were implemented in R (see also Data S1). Details on the used packages can be found in Appendix S1: Table S1.

Niche comparison and dynamics

To compare the ecological (climatic, to be precise) niches of *L. camara* and *P. juliflora* in their global, native, and Eastern African invaded ranges, we followed the methodology proposed in Broennimann et al. (2012). For each species, we performed a principal component analysis (PCA) using the eight most influential and diverse species-specific bioclimatic variables identified during bioclimatic variable reduction, combined with the species occurrence data and the reduced final selection of species pseudo-absence data. Principal component analysis discriminates between the ecological niches of the chosen presence data and pseudo-absences and has been shown to accurately identify niche overlaps as well as niche differences and shifts (Broennimann et al. 2012, Goncalves et al. 2014). The two first principal components explained 64.55% and 59.94% of the environmental variance in the data for *L. camara* and *P. juliflora*, respectively. Following the PCA, again for each species, we divided the relevant environmental space into a grid of 500 × 500 cells and converted the occurrence points into occurrence densities using a kernel smoothing function. The pseudo-absence data were then used to estimate the density of available environments in each cell of environmental space. Based on the two densities, we estimated an occupancy index, thus enabling unbiased comparison of species occurrence densities. The occupancy index was plotted on the environmental space to delimit the ecological niches occupied by the two investigated species in their respective global and invaded ranges. We considered the entire ecological niches in both ranges and included 95% of the

global and Eastern African niche occurrences, excluding marginal climates in the two data sets to account for data inaccuracies. Additionally, we calculated the principal components of the first introduction sites of *P. juliflora* in Kenya and Ethiopia to understand where they are positioned in the Eastern African niche and whether they overlap or rather complement each other. This was not possible for *L. camara*, as it was introduced to Eastern Africa much earlier, with single plants imported as ornamental plants, and there is no detailed information on distinct introduction sites.

We used Schoener's *D* to compare niche overlaps between climatic spaces. Schoener's *D* ranges from 0 to 1, with 1 representing two identical niches (Schoener 1970). In order to test whether the Eastern African niche of invasive *P. juliflora* changed relative to its global niche, we tested them for equivalence and similarity (Warren et al. 2008). In the equivalence test, all occurrences (global and regional) are partitioned randomly, using 1000 replicates, extracting two new occurrence samples of the same size as the original occurrence data set and calculating *D*. The null distribution of the simulated *D* is then compared to the original observed *D* in a one-sided similarity test. The null hypothesis is rejected if $P < 0.05$ (i.e., niches are not identical). In the similarity test, the global niche is compared with a random selection, again using 1000 replicates, of occurrences drawn from the background of the Eastern African invaded range. The null distribution of the simulated *D* is then again compared to the original observed *D*. The null hypothesis is rejected if $P < 0.05$ (i.e., niches are more similar than random).

We calculated niche overlap of the ecological niches excluding 5% marginal data to account for inaccuracies in the data (e.g., taxonomic variability). Moreover, we calculated the proportions of the total niche space (in the global, respectively native, and the Eastern African invaded ranges) that occurred in both ranges (stability), were occupied only by the global (resp. native) niche (unfilling), and were occupied only by the invasive niche (expansion; Petitpierre et al. 2012, Guisan et al. 2014). This study's focus was on the comparison of the global with the Eastern African niche. However, we additionally calculated the comparison

between the native and the Eastern African niche for the current climate to understand the contribution of climates from other invaded areas and whether they differ from the Eastern African climates. The results of the native–Eastern African niche comparison can be found in Appendix S1: Fig. S5. All calculations were done using functions available in the ecospat R package (version 2.1.1; Cola et al. 2017).

To assess the stage of invasion, we compared the probabilities calculated by the regional and the global ensemble models, which represent the realized regional and global niches, respectively. This enabled us to derive the current stage of invasion for the two species (Gallien et al. 2012). Four situations, represented by four quadrants, can be compared if the regional model probabilities are plotted against the global model probabilities. Gallien et al. (2012) proposed that the four quadrants represent four stages of invasion: Regional species presence points in areas where the regional and the global niche overlap (top right quadrant) suggest that the regional population is stabilizing. Presence points that are in the Eastern African niche but outside the global niche (top left quadrant) suggest that the regional population might be undergoing a relatively rapid local adaptation process. Presence points that are in the global niche but outside the Eastern African niche (bottom right quadrant) suggest that the geographic areas where they occur might still be colonized. Finally, presence points outside both the regional and the global niche may be considered as populations that were introduced to an unsuitable habitat and are unlikely to stabilize or increase.

RESULTS

Model performance and variable selection

In our attempts to model the global niche of *P. juliflora*, the defined performance requirements were met by the two BRT models and one of the RF models, with TSS ranging between 0.50 and 0.61 and AUC between 0.87 and 0.97. For *L. camara*, only the RF models met the performance requirements, with TSS ranging between 0.57 and 0.59 and AUC between 0.94 and 0.95. These respective models were used to generate one ensemble global niche model each for *P. juliflora* and *L. camara*.

Among the Eastern African niche models for *P. juliflora*, the two BRT models and one of the RF models met our performance requirements, with TSS ranging between 0.50 and 0.51 and AUC = 0.99 for all three models. For the Eastern African niche of *L. camara*, the requirements were met by the two BRT models and the two RF models, with TSS ranging between 0.57 and 0.66 and AUC between 0.98 and 0.99. These respective models were used to generate ensemble Eastern African niche models for the two species. For *P. juliflora*, we achieved the best modeling results using 15 variables, and for *L. camara*, we achieved the best results using a set of 9 variables (see also Table 1).

In the case of *P. juliflora*, bio9, bio19, distance to waterbodies, NDVI of mid-April (end of dry season in all three countries), and the Human Footprint Index contributed most to the regional model. In the case of *L. camara*, bio12, bio5, the Human Footprint Index, and NDVI of mid-August (dry season in Kenya and Tanzania, wet season in Ethiopia) contributed most to the regional model.

Niche analysis considering current and future climates

The global and Eastern African niches of both species overlap to a large extent. However, we found a slight expansion into new environments for both species when a certain percentage of marginal climates (at least 10% for *P. juliflora* and at least 5% for *L. camara*) are excluded. Fig. 1a, b shows the niche overlap when 95% of data are considered. Niche unfilling ranges between 46% (considering 100% of the data) and 68% (considering 85% of the data) for *P. juliflora* and between 64% and 86% (analogous settings) for *L. camara* (see also Table 2). Niche expansion is low or zero for both species, ranging up to 3.3% for *P. juliflora* and 2.5% for *L. camara*. For both species, the similarity and equivalency tests are not significant if 95% of the data are considered. The global and Eastern African niches are thus not more similar than randomly expected (*P. juliflora*: $P = 0.447$, Schoener's $D = 0.1866$; *L. camara*: $P = 0.091$, Schoener's $D = 0.124$), and they are not identical (*P. juliflora*: $P = 1$; *L. camara*: $P = 1$).

The Eastern African niche centroid of *P. juliflora* moved toward lower precipitation of driest, warmest, and coldest quarter (bio17,

bio18, bio19) but toward higher precipitation seasonality (coefficient of variation; bio15; Fig. 1c). The Eastern African niche centroid of *L. camara* moved toward a higher mean diurnal temperature range (bio2) and higher maximum temperatures of the warmest month (bio5), as well as toward lower precipitation values of the driest month (bio14).

Comparison between the native range and Eastern African occurrences (excluding 5% of marginal climates) produces similar results for *P. juliflora*. The two niches overlap by 23%. No niche expansion is observed, although the niche boundaries are close. Niche unfilling is 59%. For *L. camara*, the overlap is 31%, with a niche unfilling of 57%. The results suggest that the niche expanded by 3% toward lower precipitation values and a higher annual temperature range (see Appendix S1: Fig. S5).

Schoener's D and niche unfilling change for both species if we use climate data from two future climate scenarios. We used a more moderate scenario (mp45) and a more extreme one (mp85; see *Spatial data* for details). Schoener's D increases under both, whereas niche unfilling decreases. If we again consider only 95% of the data, excluding marginal climates, we obtain Schoener's D values of 0.43 (mp45) and 0.47 (mp85) for *P. juliflora* and 0.27 (mp45) and 0.28 (mp85) for *L. camara*. An expansion into new environments can be observed for both species and both scenarios. In the case of *P. juliflora*, under the more moderate climate scenario it ranges between 9% (if 90% of the data are considered) and 15% (85% of data considered), while under the extreme climate scenario it ranges between 1.5% (95% of data considered) and 15% (85% of data considered). For *L. camara*, the more moderate climate scenario suggests niche expansion between 1% (90% of data considered) and 6% (85% of data considered), while the extreme scenario suggests a niche expansion of 3% only if no more than 85% of the data are considered (see also Table 3).

The niche unfilling for the moderate climate scenario ranges between 17% (if 100% of the data are considered) and 34% (85% of data considered) for *P. juliflora* and between 33% and 71% for *L. camara* (analogous settings). The extreme climate scenario leads to niche unfilling ranging between 14% (100% of data

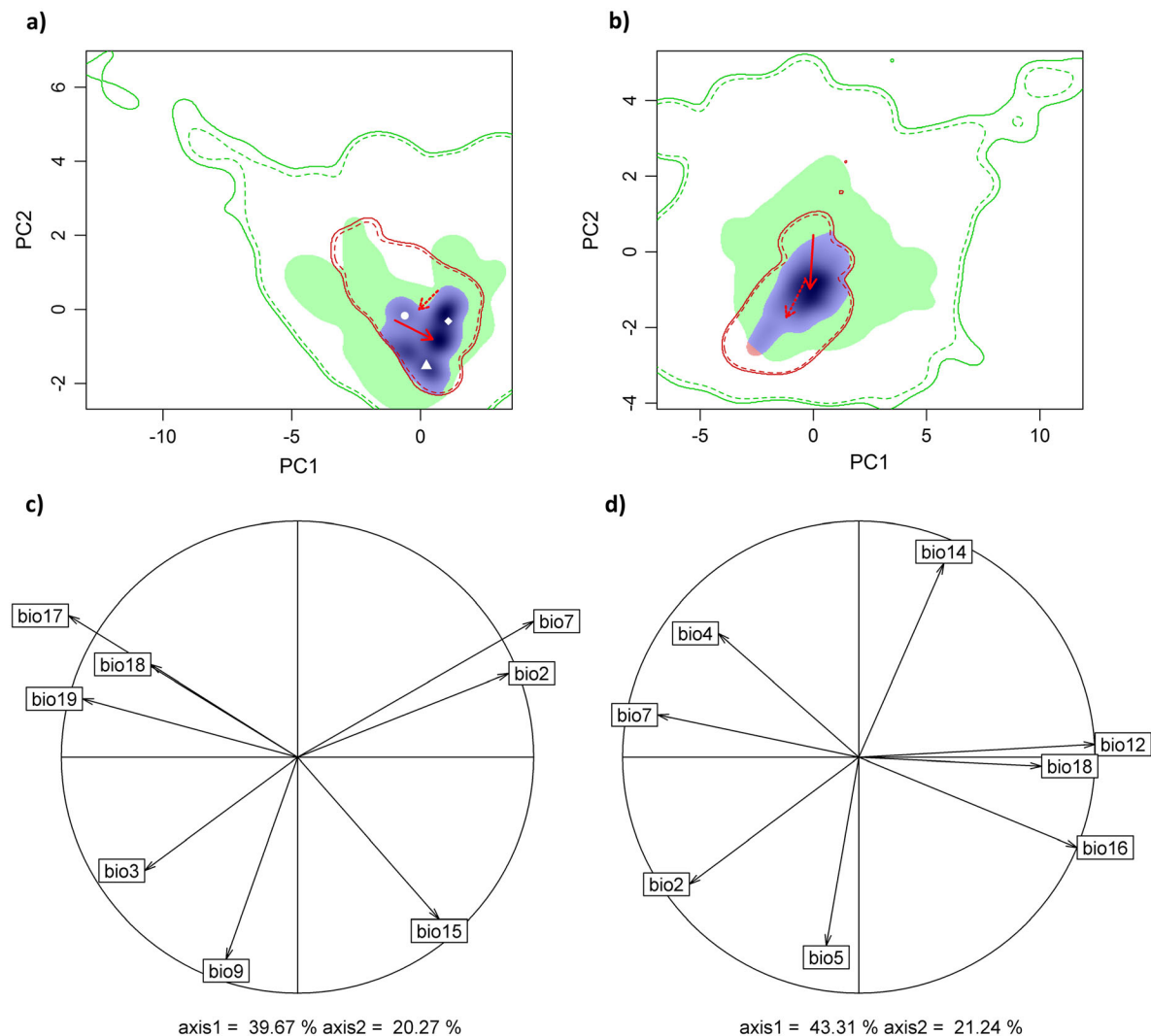


Fig. 1. Niche dynamics of *Prosopis juliflora* (a) and *Lantana camara* (b), comparing global with invaded Eastern African niches under current climate (considering 95% of the data for each niche). Unfilled areas are shown in green, stable areas in blue, and expansion areas in red. Solid and dashed lines represent the results using 100% and 90%, respectively, of the available occurrence and pseudo-absence data to delineate the global niche (green lines) and the Eastern African niche (red lines). The red solid arrow indicates the difference between the global and the Eastern African niche centroid. The red dashed arrow indicates the difference between the global and the Eastern African environmental (background) extent. The position of the first introduction sites of *P. juliflora* in Eastern Africa in the ecological niches is indicated by the white circle (Baringo, Kenya), diamond (Bura, Kenya), and triangle (Afar, Ethiopia). The principal component analysis correlation circle plots for *P. juliflora* (c) and *L. camara* (d) show the contribution of each bioclimatic variable in the niche space to the first and second principal components. The abbreviations of the bioclimatic variables are explained in Table 1.

considered) and 42% (85% of data considered) for *P. juliflora* and between 35% and 69% for *L. camara* (analogous settings; Fig. 2; see also Table 3).

Stage of invasion

To complement the niche analysis considering not only global climate data but also additional environmental data for the regional model, we

Table 2. Summary of niche dynamics results from the presented niche comparisons considering current climate conditions.

Species	Percent occurrence data considered	Stability	Unfilling	Expansion
Global vs. Eastern African niche, current climate (considering 85–100% of occurrence data)				
<i>Prosopis juliflora</i>	85%	0.966	0.681	0.033
	90%	0.989	0.634	0.011
	95%	1.000	0.586	0.000
	100%	1.000	0.465	0.000
<i>Lantana camara</i>	85%	0.975	0.859	0.025
	90%	0.974	0.840	0.026
	95%	0.995	0.786	0.005
	100%	1.000	0.638	0.000
Native vs. Eastern African niche, current climate (considering only 95% of occurrence data)				
<i>P. juliflora</i>	95%	1.000	0.585	0.000
<i>L. camara</i>	95%	0.963	0.565	0.037

Table 3. Global vs. Eastern African niche, future climate scenarios mp45 and mp85, considering 95% of occurrence data.

Species	Climate scenario	Stability	Unfilling	Expansion
<i>Prosopis juliflora</i>	mp45	0.991	0.197	0.009
	mp85	0.984	0.194	0.016
<i>Lantana camara</i>	mp45	1.000	0.514	0.000
	mp85	1.000	0.477	0.000

compared our developed regional and global model predictions in a scatterplot. This enabled us to see how well the regional presence points match the realized Eastern African niche and, more interestingly, how well they match the global niche—which we modeled based on global presences but excluding presences in the greater study region. The four quadrants in the scatterplot represent four distinct situations: stabilization, adaptation, colonization, and isolation (Fig. 3). Looking at the distribution of *P. juliflora* (yellow) and *L. camara* (blue) presence points, we can make the following observations: For both species, the majority of presence points are found in the top right quadrant, indicating that they match both niches well and are stabilizing. However, some of the *P. juliflora* and *L. camara* presence points are found in the top left and bottom right quadrants, indicating that while both species are still filling the modeled global niche in Eastern Africa, they are

also adapting to new regional conditions. This is more the case for *P. juliflora* (global model median = 0.7511; regional model median = 0.9899) than for *L. camara* (global model median = 0.8391; regional model median = 0.9987), indicating that *L. camara* is closer to reaching a quasi-equilibrium, whereas *P. juliflora* is still filling, but at the same time also expanding its Eastern African niche.

Current potential suitable habitats

The area that the models predict to be current suitable habitat for *P. juliflora* is much smaller than that predicted to be suitable for *L. camara* (Figs. 4, 5, Table 4). The globally modeled suitable habitat for *P. juliflora* mostly overlaps with the regional model; only in Tanzania does the global model consider an additional 15% of the country's territory to be suitable compared to the regional model. The regional model for *P. juliflora* predicts larger suitable habitats than the global model, considering an additional 15.25% of Ethiopia, 16.72% of Kenya, and 19.78% of Tanzania to be suitable. The Ethiopian and Kenyan lowlands and the semiarid-to-arid regions in the Kenyan highlands are largely considered suitable habitat for *P. juliflora* by both the regional and the global ensemble models. These regions are known to be heavily affected by *P. juliflora* invasion. In Tanzania, the species has been identified only recently, mostly in the north of the country. The output of both the global and

the regional model suggests that a large part of Tanzania may be suitable habitat for *P. juliflora*, thus indicating that the plant constitutes a potential threat to the country.

For *L. camara*, the suitable area predicted by the regional model largely falls within that predicted by the global model (Fig. 5). However, the global model considers a much larger area suitable than the regional model does, with 51.34% of the total area of Ethiopia, Kenya, and Tanzania overlapping and another 40.66% considered suitable only by the global model (Table 4). In Ethiopia, the lowland areas are considered unsuitable by the more refined regional model. The same can be observed in Kenya, where 34.93% of the country is considered suitable by both models, while the global model considers an additional 62.62%—mostly the semiarid-to-very arid areas of Turkana County and the lowlands—suitable. Similar patterns also occur in South Sudan and Somalia. In Tanzania, the two models match well, with 72.93% of the country's total area considered suitable habitat for *L. camara* by both models; an additional 14.88% is considered suitable only by the global model and 6.41% only by the more refined regional model.

Future potential suitable habitats

The ensemble models predict range changes for both *P. juliflora* and *L. camara* when using the two selected future climate scenarios rather than current climate data (Figs. 6–9). The changes in suitable habitat for *P. juliflora* under future climate scenarios are substantial. The models predict Tanzania to be most heavily affected by an increase in suitable habitat (mp45, 18.64%; mp85, 12.19%). A decrease can be expected above all in Tanzania (mp45, 7.18%; mp85, 9.84%), followed by Ethiopia (mp45, 5.36%; mp85, 6.46) and Kenya (mp45, 5.09%; mp85, 7.52%).

Expected changes in suitable habitat for *L. camara* are smaller. Among our three study countries, Tanzania appears to be most heavily affected by an increase (mp45, 3.04%; mp85, 3.92%). Notable suitable habitats were also modeled for the neighboring countries of Somalia and South Sudan. A decrease in habitats may be expected above all in Tanzania (mp45, 10.16%; mp85, 10.25%) and Ethiopia (mp45, 5.00%; mp85, 4.03%).

DISCUSSION

The comparative assessment of the ecological niches, stages of invasion, and potential distribution of *P. juliflora* and *L. camara* in Eastern Africa revealed patterns that are consistent across the modeling approaches taken and match the different invasion histories. Our results indicate that *P. juliflora* invasion in Eastern Africa is still at an early stage and that it is likely to expand its current geographic range significantly if left uncontrolled. *L. camara*, by contrast, appears to be approaching a pseudo-stable equilibrium in Eastern Africa. However, the different approaches also produced conflicting results. For example, while the inclusion of marginal climates in the ecological niche analysis suggests niche conservatism for *P. juliflora*, analysis of the stage of invasion hints at a rapid adaptation of this species to novel environmental conditions. Further, it is worth noting that the global geographic model predicts a much larger area to be suitable for *L. camara* than the Eastern African model.

Niche analyses and stages of invasion

Invasive species may respond to new environments in various ways, for example, with niche conservatism, with niche expansion along multiple or very specific climatic or other environmental variables, or by shifting into a new niche completely different from the native one (Petitpierre et al. 2012, Guisan et al. 2014). In the case of *P. juliflora*, differences between the global and Eastern African niches can mostly be attributed to unfilling of the global niche. If more than 5% of extreme climates are removed from both niches, a very small amount of the Eastern African niche exceeds the global one. This suggests, first, that *P. juliflora* has not yet reached an equilibrium in Eastern Africa, and second, that some individuals might eventually succeed in adapting to more marginal or even new climatic conditions. The local niches of the three locations where *P. juliflora* was first introduced complement each other and coincide in environmental space with the highest Eastern African niche densities found for *P. juliflora* today. The three locations where plantations were originally established differ in both geographic and environmental space, and the Eastern African niche is expanding outward in environmental space

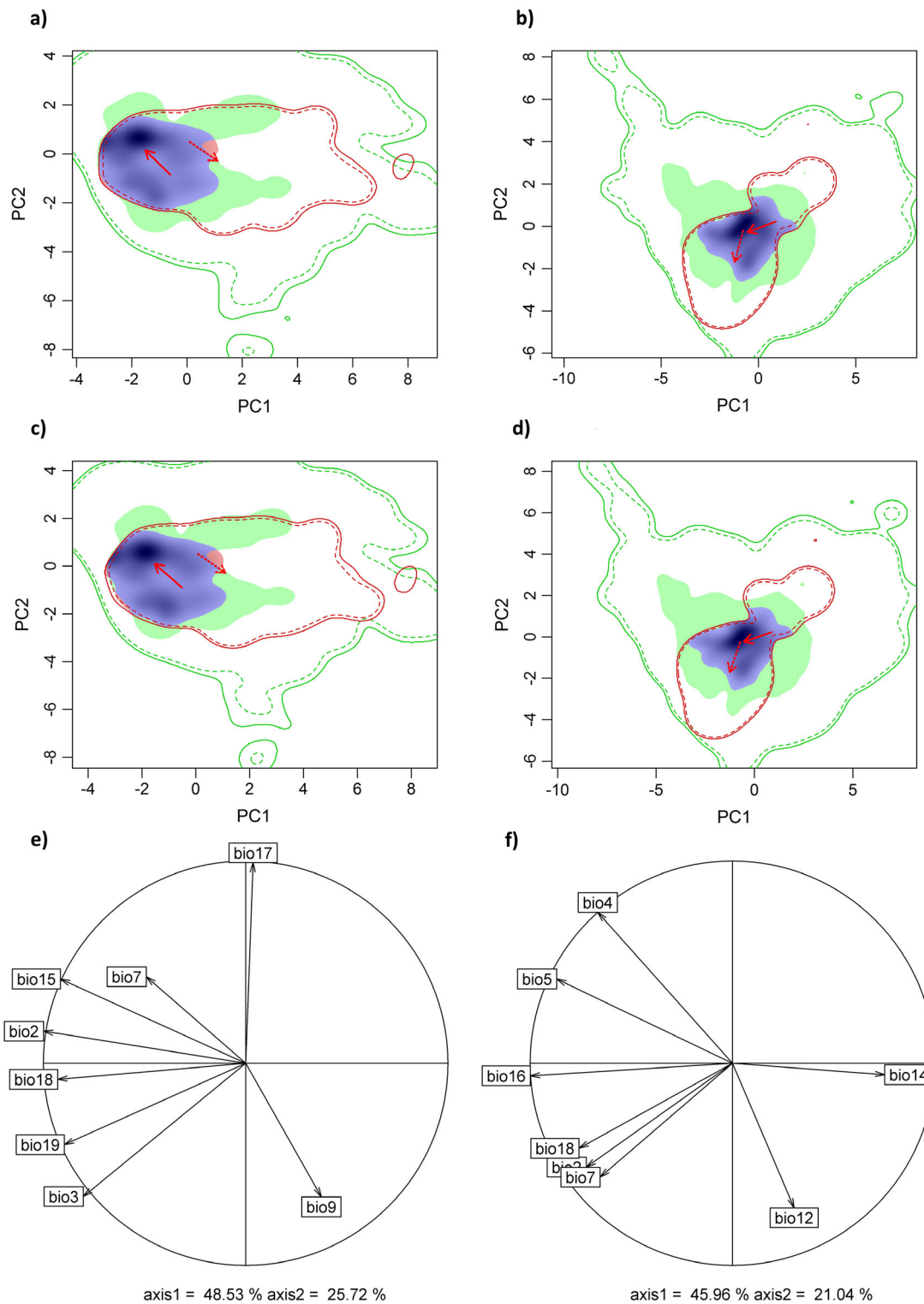


Fig. 2. Niche dynamics of *Prosopis juliflora* (a, c) and *Lantana camara* (b, d) comparing global with invaded East African niches under two future climate scenarios (considering 95% of the occurrence data for each niche).

(Fig. 2. Continued)

Unfilled areas are shown in green, stable areas in blue, and expansion areas in red. Solid and dashed lines represent the results using 100% and 90%, respectively, of the available occurrence and pseudo-absence data to delineate the global niche (green lines) and the Eastern African niche (red lines). The red solid arrow indicates the difference between the global and the Eastern African niche centroid. The red dashed arrow indicates the difference between the global and the Eastern African environmental (background) extent. The position of the first introduction sites of *P. juliflora* in Eastern Africa in the ecological niches is indicated by the white circle (Baringo, Kenya), diamond (Bura, Kenya), and triangle (Afar, Ethiopia). The principal component analysis correlation circle plots for *P. juliflora* (e) and *L. camara* (f) show the contribution of each bioclimatic variable in the niche space to the first and second principal components. The abbreviations of the bioclimatic variables are explained in Table 1.

from each of the three locations (Fig. 1a). Hence, the results of our comparison of global with Eastern African niches might be misinterpreted in terms of an overestimation of actual niche filling in each individual country if niche dynamic plots are not linked to geographic space. This may particularly be the case where invasive species were deliberately introduced and planted at specific locations, as was the case for numerous exotic woody plant species (Richardson et al. 2014). To link ecological and geographic information, we therefore suggest taking a nested approach by plotting local ecological niches separately and

assessing how well they match the regional ecological niche. We provide two examples of local niches for Ethiopia, where the highest levels of *P. juliflora* invasion are found in Afar, a semiarid-to-arid region in the Ethiopian lowlands. Thus, for Afar we would have expected a higher rate of niche filling as compared to the one we actually found (stability 1.000, unfilling 0.834, expansion 0.000; Fig. 10a). In contrast, for *P. juliflora* occurrences in the country's very climatically diverse highlands, we would have expected a lower rate of niche filling compared to what we found (stability, 0.989; unfilling, 0.146; expansion, 0.011; Fig. 10b). In this example from the Ethiopian highlands, we even observed a slight niche expansion.

The PCA correlation circle plots suggest that compared to the global niche, the Eastern African niche centroid has moved toward lower precipitation values (bio17, bio18, bio19) but higher precipitation seasonality (bio15). With expected climatic changes, the Eastern African niche is likely to expand toward a higher mean diurnal temperature range (bio2), higher precipitation seasonality (bio15), and higher precipitation values during the warmest and coldest quarters.

The results were not significantly affected when we compared the Eastern African niche with the native instead of the global niche. However, the Eastern African niche is closer to expanding the native niche than the global one, suggesting that the global niche contains climates not present in the native niche and thus might represent a closer approximation of the elusive fundamental niche (Broennimann et al. 2007, Beaumont et al. 2009). Oliveira et al. (2018) performed a similar study comparing the native

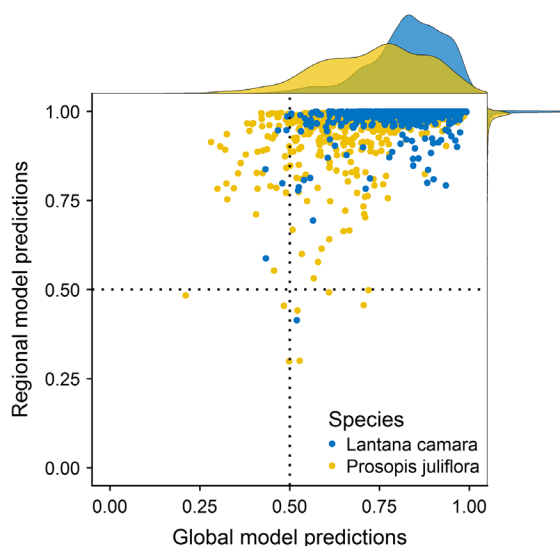


Fig. 3. Scatterplot and histograms of observed presence points of *Prosopis juliflora* (blue) and *Lantana camara* (yellow), comparing the probabilities predicted by the regional and the global ensemble models.

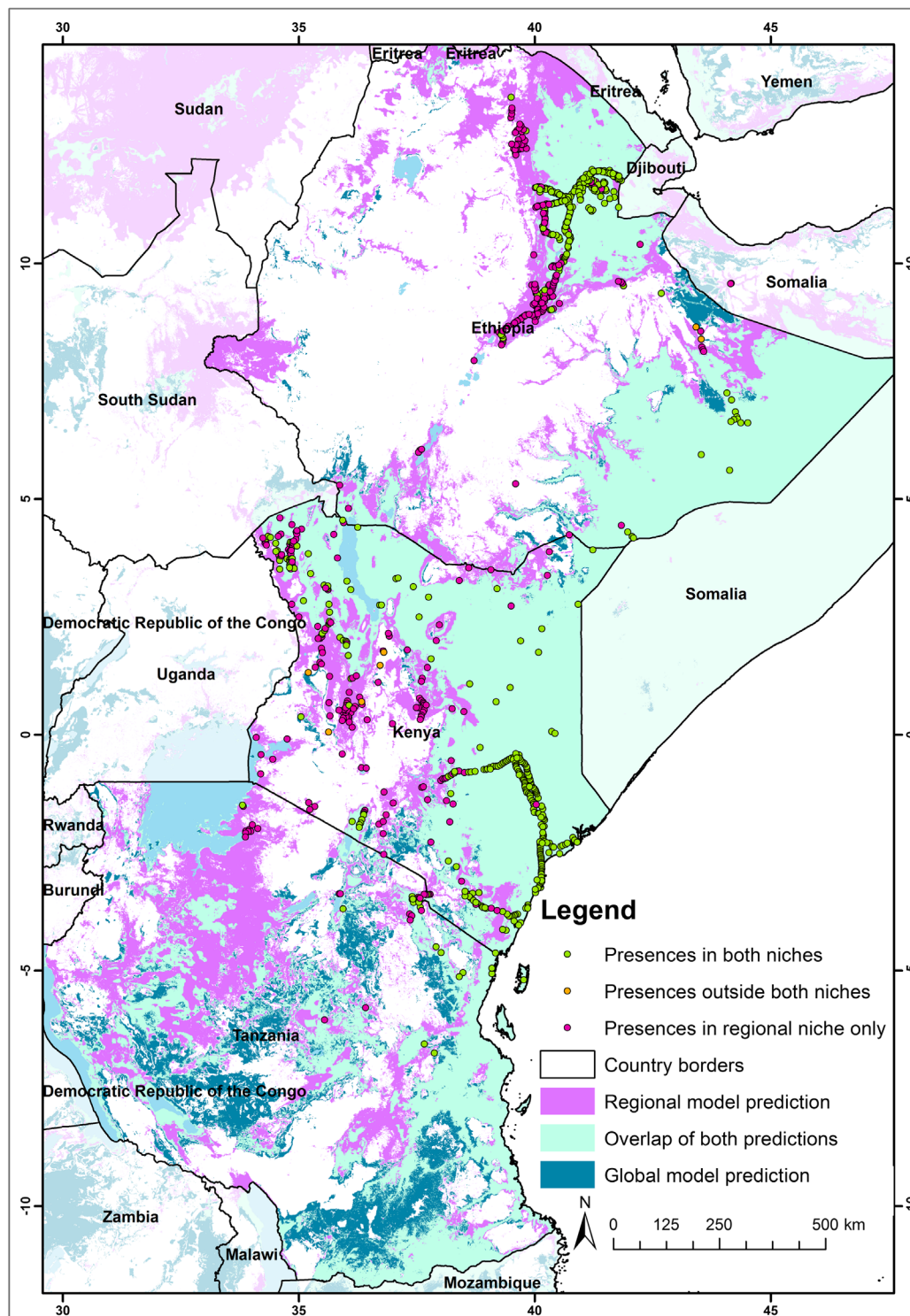


Fig. 4. Geographic representation of the modeled global (dark cyan) and regional (magenta) niches, as well as the overlapping areas of the two modeled niches (cyan) for *Prosopis juliflora*. Presence points of the two species are shown as colored dots, with colors indicating in which niche(s) they occur.

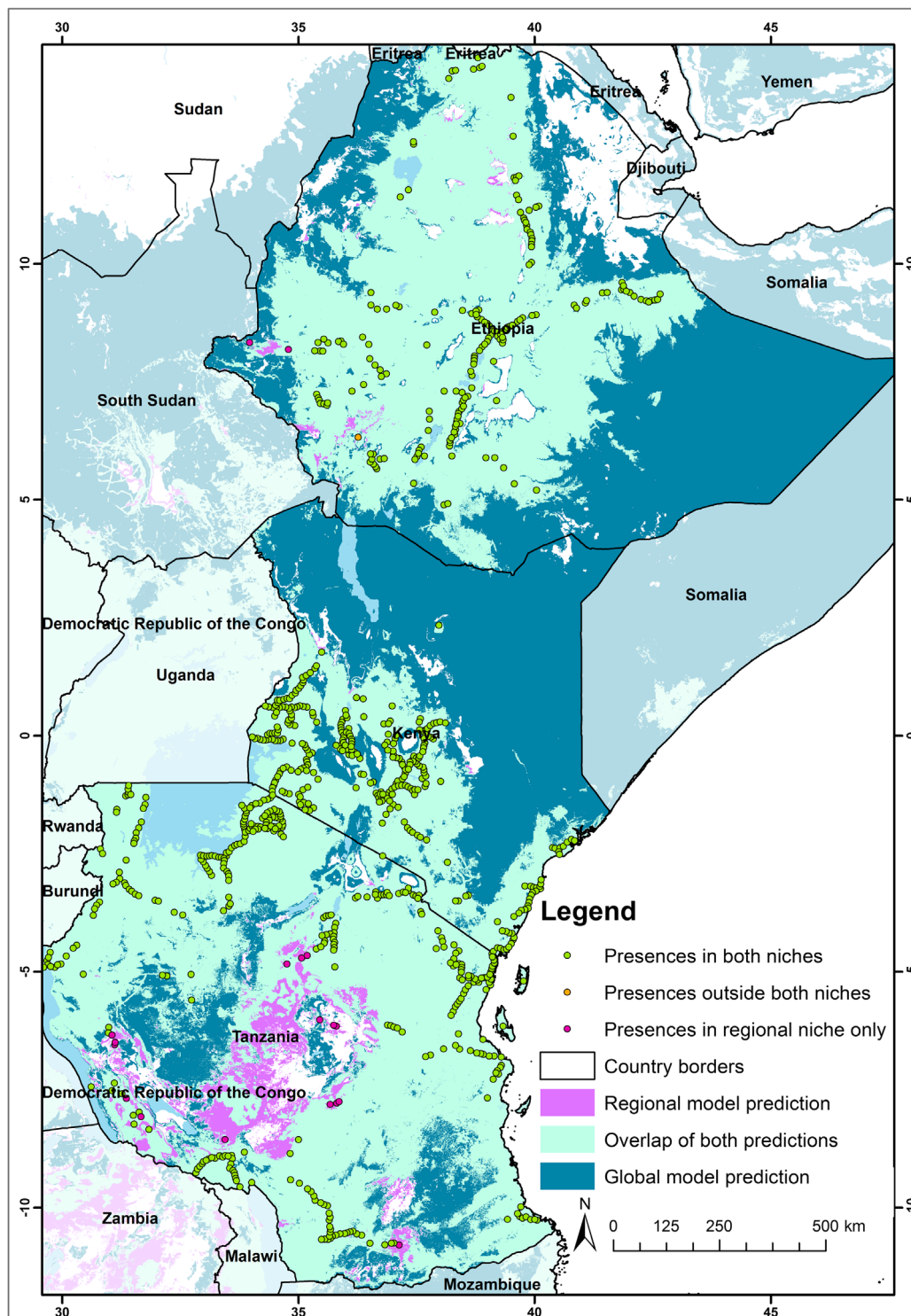


Fig. 5. Geographic representation of the modeled global (dark cyan) and regional (magenta) niches, as well as the overlapping areas of the two modeled niches (cyan) for *Lantana camara*. Presence points of the two species are shown as colored dots, with colors indicating in which niche(s) they occur.

Table 4. Area (km² and percentage shares) of each individual country considered suitable habitat by none, the global, the regional, or both models.

Species	Category	Ethiopia		Kenya		Tanzania	
		Area (km ²)	Area (%)	Area (km ²)	Area (%)	Area (km ²)	Area (%)
<i>Lantana camara</i>	None	85,643.35	7.57	13,975.93	2.38	54,733.46	5.78
	Only regional	4950.62	0.44	392.23	0.07	60,660.92	6.41
	Only global	460,176.45	40.66	367,193.54	62.62	140,895.58	14.88
	Both	581,118.70	51.34	204,856.25	34.93	690,489.69	72.93
<i>Prosopis juliflora</i>	None	611,867.77	54.06	116,909.30	19.94	319,345.13	33.73
	Only regional	172,659.09	15.25	98,070.29	16.72	187,315.84	19.78
	Only global	24,772.93	2.19	12,163.59	2.07	144,292.12	15.24
	Both	322,599.36	28.50	359,280.02	61.27	295,843.23	31.25

range of *P. juliflora* with an area in Brazil where the species is invasive. They found climatic niche conservatism with an unfilling rate of 40% and no observed expansion. Unfortunately, they provide no information regarding the percentage of marginal climates excluded or the contribution of each bioclimatic variable they used (i.e., PCA correlation circle plots).

Differences in the ecological niches of *L. camara* can mostly be attributed to unfilling of the global niche by the Eastern African niche. The Eastern African niche exceeds the global one when more than 5% of marginal climates are excluded. This indicates a shift toward new climatic conditions. Like for *P. juliflora*, this suggests that some *L. camara* individuals might eventually succeed in adapting to new climatic conditions. The PCA correlation circle plots for *L. camara* indicate that the Eastern African niche has shifted toward warmer and drier climates compared to the global niche, with a small part exceeding the global niche. A similar shift in climates was observed for invasive *L. camara* in India (Goncalves et al. 2014), whereas the same study predicted no shift in Africa and Australia. This may be because it used African occurrence points mostly from Southern Africa and Madagascar, whereas we used occurrence points from Ethiopia, Kenya, and Tanzania. Looking at future climate scenarios, our models suggest a small expansion of the Eastern African niche of *L. camara* only when at least 10% of marginal climates are excluded; this is coupled with a shift of the niche toward higher annual and mean diurnal temperature ranges and higher precipitation during the warmest quarter.

The Eastern African niche of *L. camara* showed a similar expansion when compared to the native and the global niches. Compared to the native niche, the Eastern African niche clearly shifted toward a higher temperature annual range, mean diurnal range, and seasonality, but toward lower precipitation values. This is surprising, as comparison with the global niche and also the results obtained by Goncalves et al. (2014) indicate a shift toward higher precipitation values. This might again indicate that the global niche contains climates not present in the native niche (Broennimann et al. 2007, Beaumont et al. 2009).

Gallien et al. (2012) proposed that comparison of the probabilities calculated by the regional and the global ensemble models helps in assessing the stage of invasion of alien species as well as their risk of spreading in the near future and that this approach is applicable to a large number of species and thus useful for biological invasion management planning. In our study, the additional comparison of the global with the regional ensemble model probabilities partially confirms the findings of the PCA-based niche analyses. The probabilities at both species' presence points are mostly positioned in the top right quadrant, meaning that they are similarly high. However, some probabilities are located in the top left and bottom right quadrants, indicating ongoing colonization and adaptation. This is more the case for *P. juliflora* than for *L. camara*, suggesting that the risk of expansion is higher for *P. juliflora* than for *L. camara*. The PCA-based niche analyses only indicated expansion when marginal climates (at least 10% for *P. juliflora* and at least 5% for *L. camara*) were excluded. Transplant experiments in Kenya revealed that

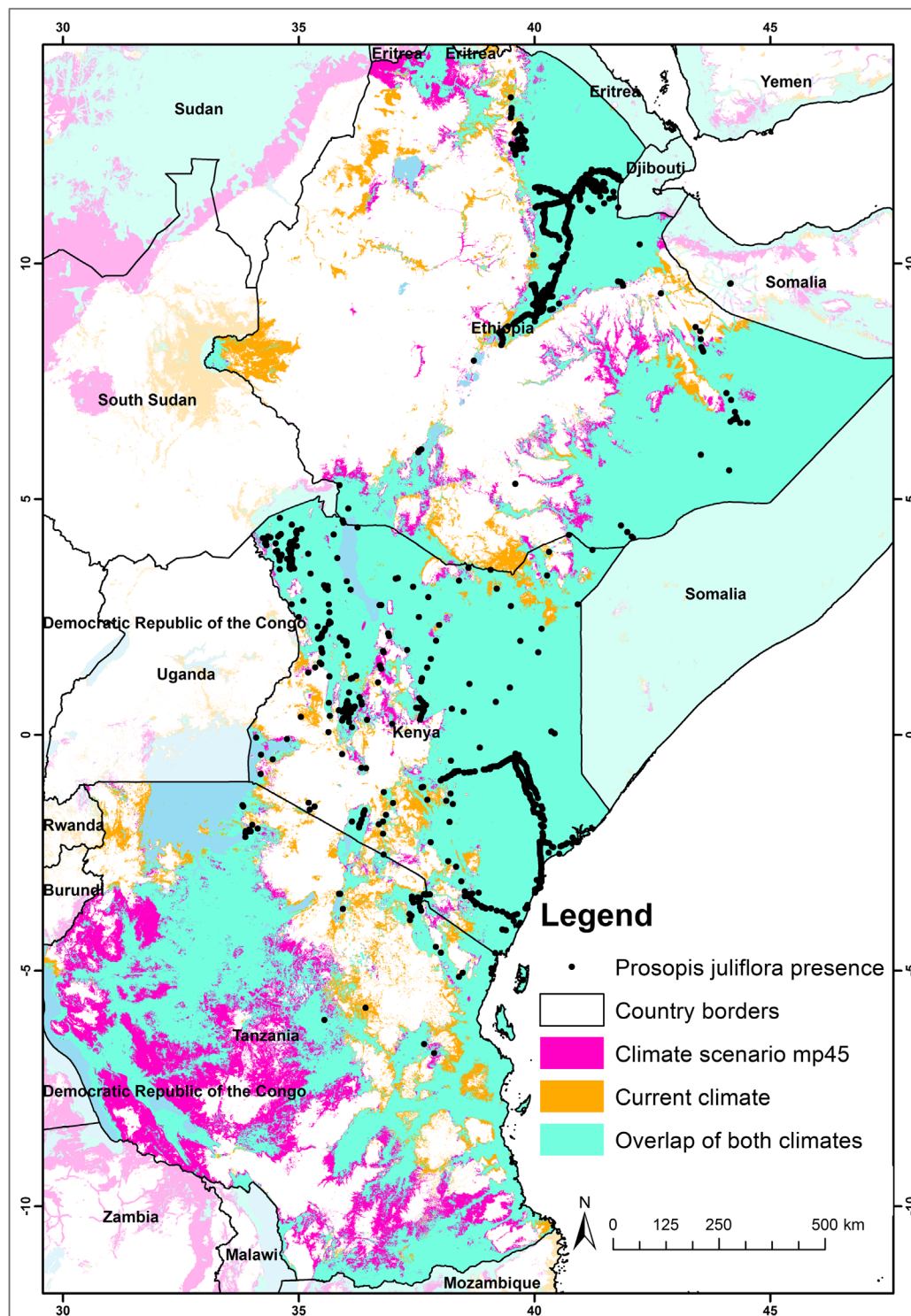


Fig. 6. Comparison of species habitat models using current climate data and future climate scenario data (mp45) for *Prosopis juliflora*. Overlapping areas are shown in cyan, future habitat gains in pink, and future habitat losses in orange.

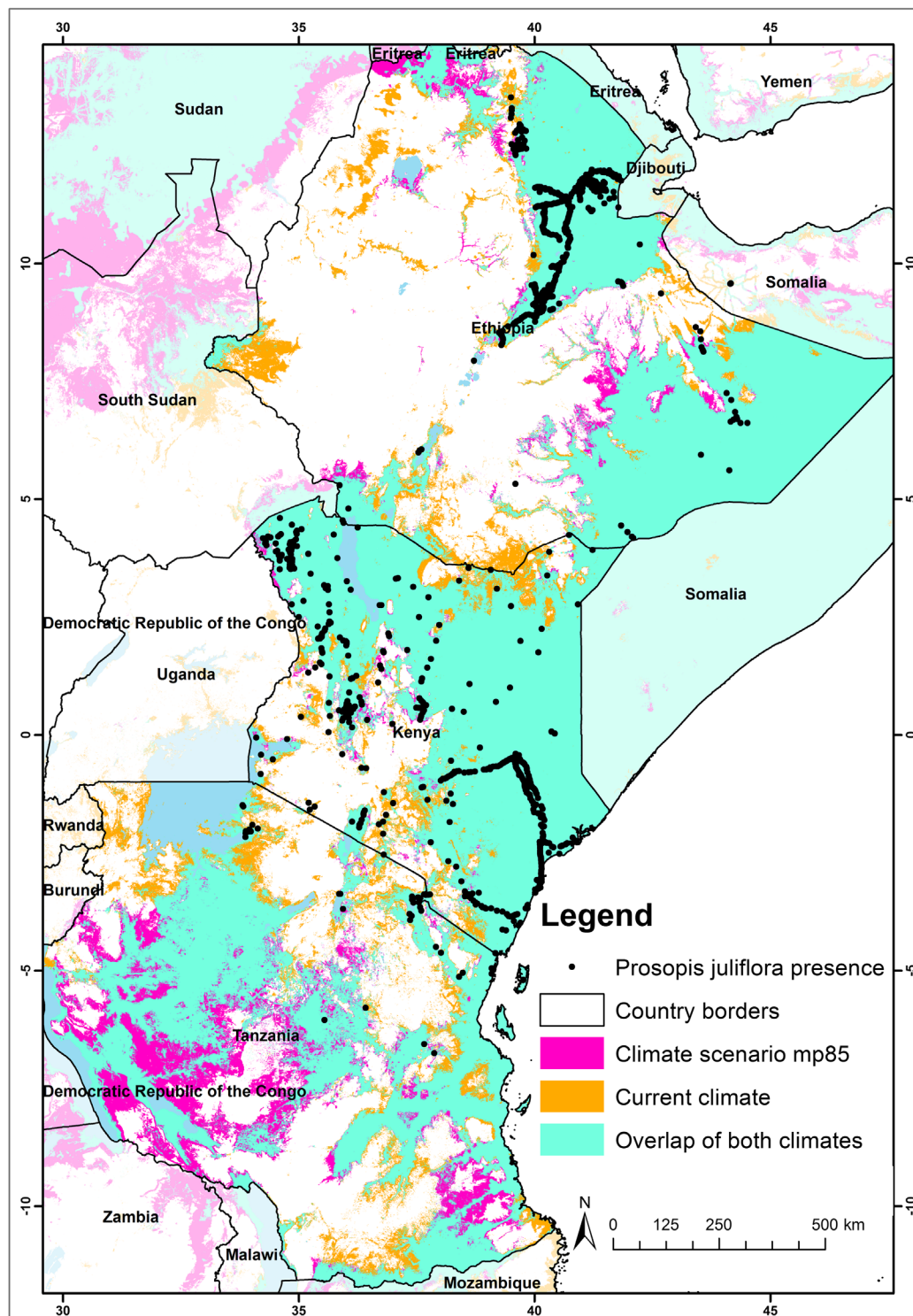


Fig. 7. Comparison of species habitat models using current climate data and future climate scenario data (mp85) for *Prosopis juliflora*. Overlapping areas are shown in cyan, future habitat gains in pink, and future habitat losses in orange.

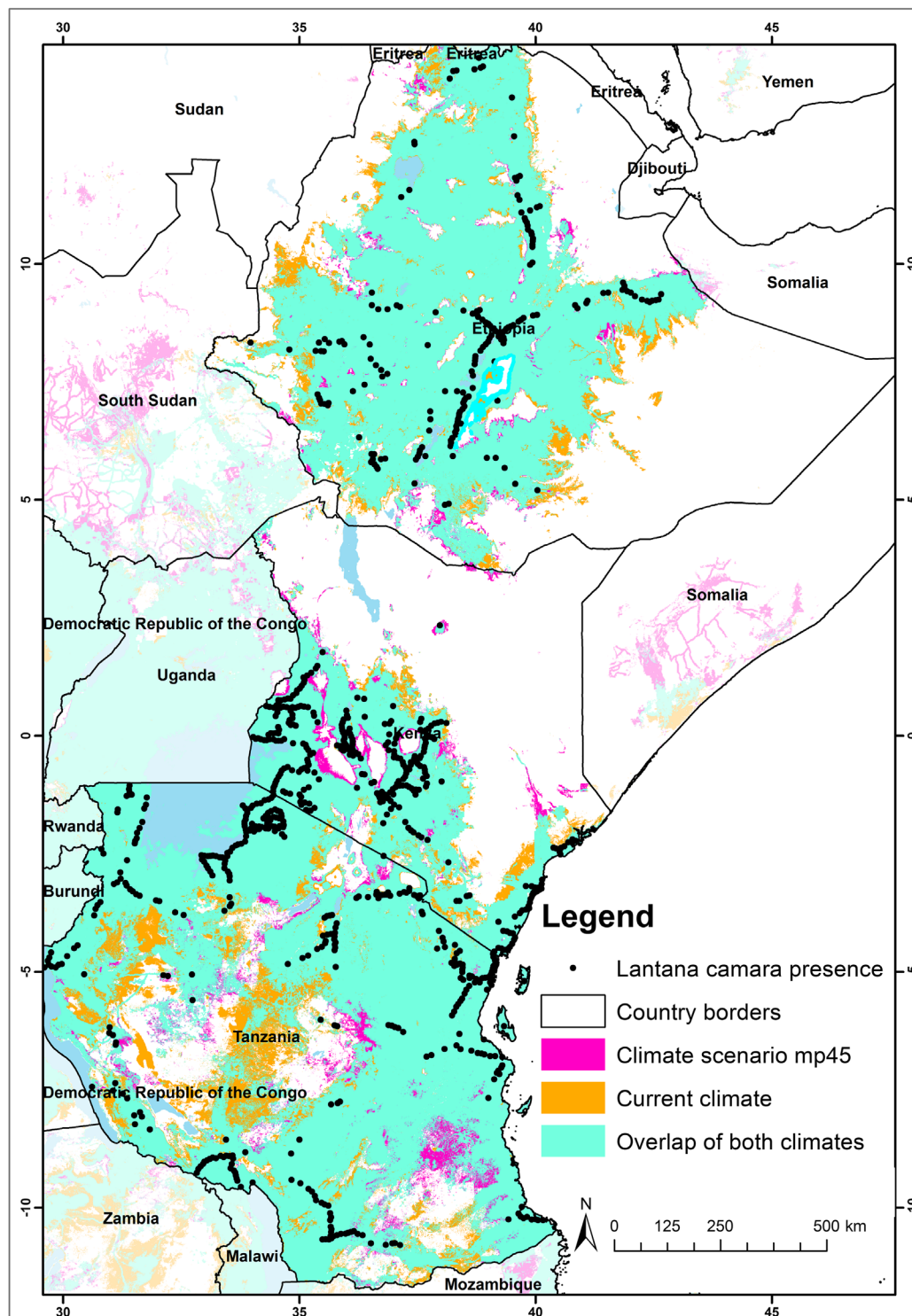


Fig. 8. Comparison of species habitat models using current climate data and future climate scenario data (mp45) for *Lantana camara*. Overlapping areas are shown in cyan, future habitat gains in pink, and future habitat losses in orange.

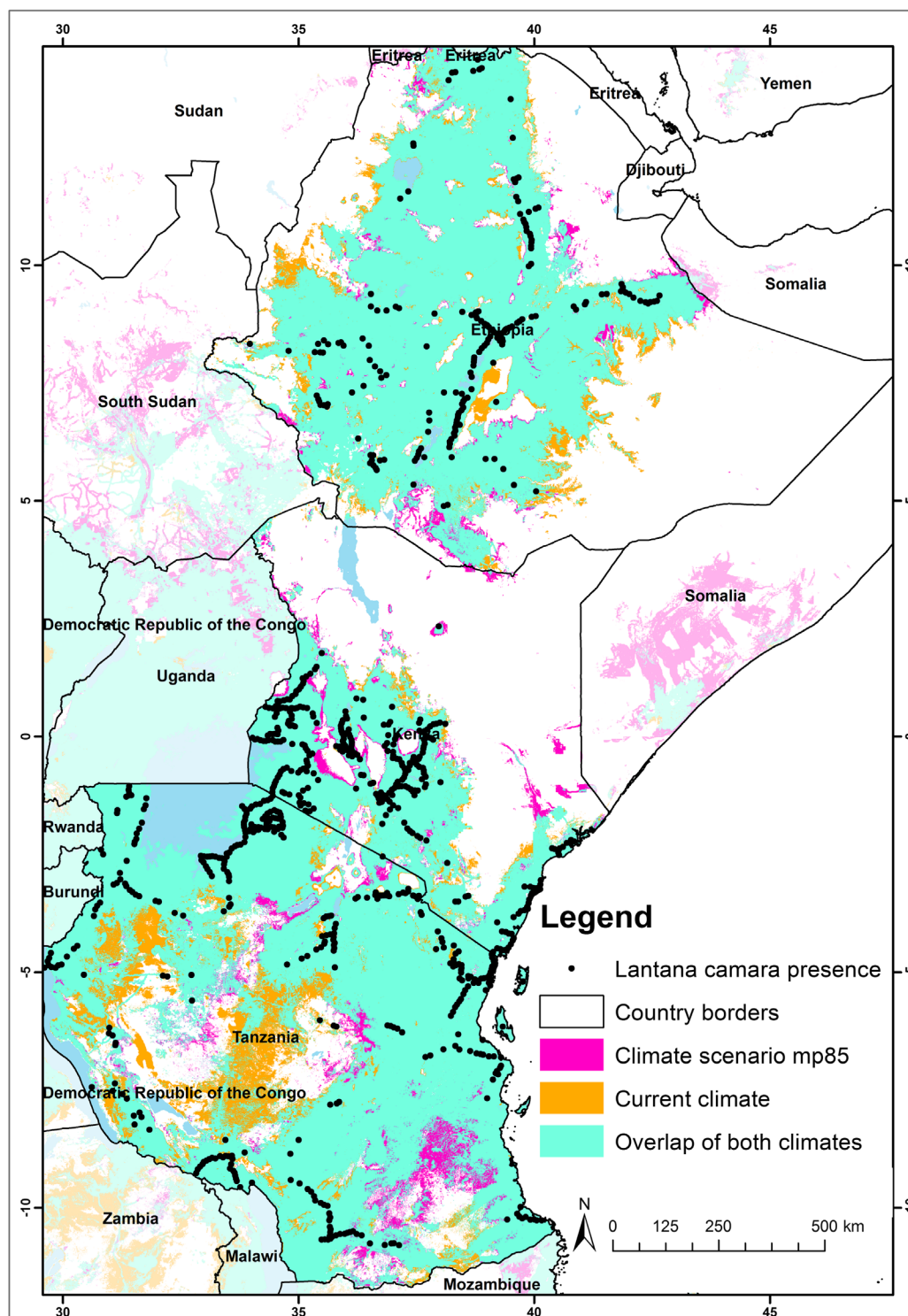


Fig. 9. Comparison of species habitat models using current climate data and future climate scenario data (mp85) for *Lantana camara*. Overlapping areas are shown in cyan, future habitat gains in pink, and future habitat losses in orange.

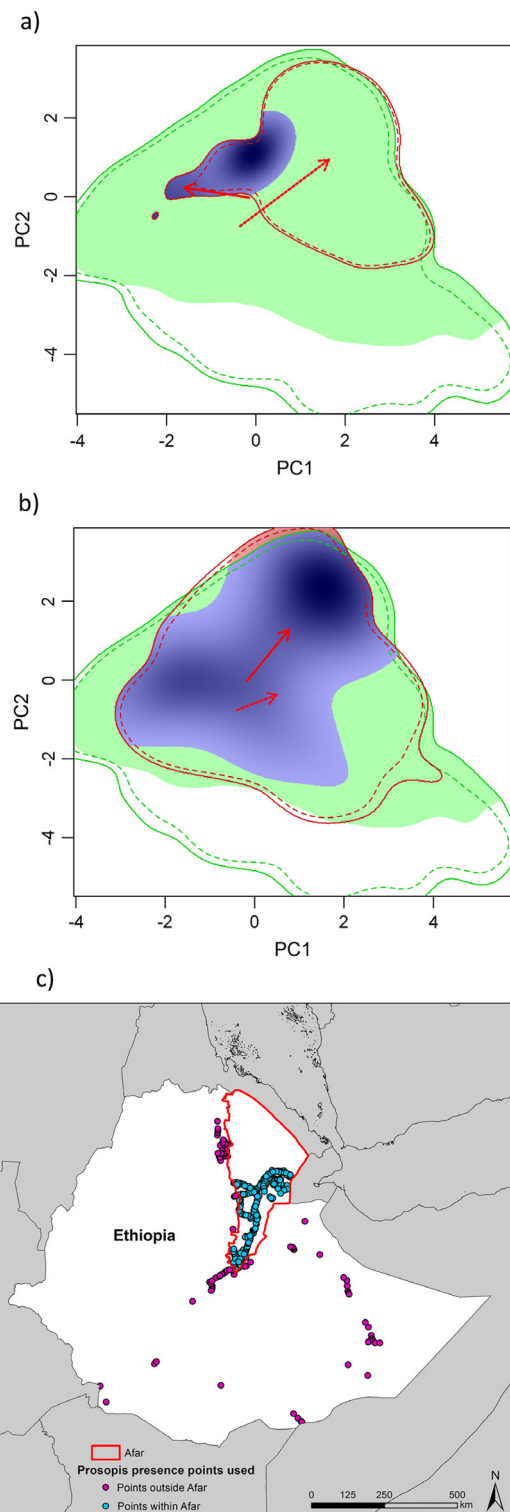


Fig. 10. Nested approach comparing (a) the local environmental niche of *Prosopis juliflora* in Afar with

(Fig. 10. Continued)

the Ethiopian climate and (b) the environmental niche of all other *P. juliflora* occurrences in Ethiopia with the Ethiopian climate. (c) *P. juliflora* occurrences used in (a) are shown in blue, and those used in (b) are shown in red. Unfilled areas are shown in green, overlap areas in blue, and expansion areas in red. Solid and dashed lines represent the results using 100% and 90%, respectively, of the available occurrence and pseudo-absence data to delineate the Ethiopian “niche” (green lines) and the “local” Afar niche (red lines). The red solid arrow indicates the difference between the national and the local niche centroid. The red dashed arrow indicates the difference between the national and the local environmental (background) extent.

P. juliflora genotypes from the invasion front differed from those originally introduced in various fitness-related traits, suggesting that *P. juliflora* may indeed be undergoing rapid post-introduction evolution (M. L. Castillo et al., unpublished manuscript). Further experimental evidence is needed to elucidate whether invasive *P. juliflora* genotypes in Eastern Africa are already capable of colonizing areas where environmental conditions are less suitable for genotypes from other parts of the global range. Another reason why our results point to more ongoing colonization and adaptation processes for *P. juliflora* than for *L. camara* may be that the global occurrence data set of *L. camara* encompasses a larger range of environmental conditions than that of *P. juliflora*.

Data accuracy considerations

The accuracy of climate variables is lower in Eastern Africa than in Northern America or Europe, as the network of meteorological stations is much coarser. Moreover, the stations are frequently out of order, resulting in incomplete climate data time series. This reduces the accuracy of spatially interpolated bioclimatic data sets. The same applies to spatial data under climate change scenarios (McSweeney et al. 2015, Klein et al. 2016). We tried to counteract these data inaccuracies by refining the regional model, using additional environmental variables and removing pseudo-absences outside the suitable habitats modeled by the global ensemble models.

Thanks to a long history of doing research in the study region, we obtained a comparably large set of *L. camara* and *P. juliflora* occurrence data containing data points from most regions in Ethiopia, Kenya, and Tanzania where *L. camara* and *P. juliflora* are currently present. However, some data gaps exist in areas that are inaccessible or areas experiencing terrorism or social conflicts. Furthermore, we expect that our data set might contain a spatial sampling bias because the majority of the data points were collected by car and, accordingly, many points were collected along travel routes. We attempted to account for this during data preprocessing. At the same time, it should be noted—and this applies particularly for *P. juliflora*—that travel routes (used by humans or animals) act as important dispersal pathways in addition to rivers.

Current and future potential suitable habitats in geographic space

In the SDM of both species, only the two machine learning algorithms BRT and RF achieved TSS >0.5, some of them reaching TSS >0.6. This corresponds to performance results obtained by other studies comparing different SDM algorithms (Araújo et al. 2005, Elith and Graham 2009, Mainali et al. 2015). While for *L. camara*, a set of 15 variables resulted in the highest TSS, a smaller set of 9 variables resulted in the highest TSS for *P. juliflora*. In this study, we did not consider AUC_{Diff}, an indicator that accounts for overfitting (Warren and Seifert 2011). However, we are confident that choosing the models based on the performance of TSS and AUC defining respective minimum thresholds provided us with the accurate models. By visualizing the modeled global niche geographically in comparison with the realized Eastern African niche, we see that mostly the semiarid-to-arid regions of Ethiopia and Kenya are currently affected, or at a high risk of being invaded, by *P. juliflora*. Recently *P. juliflora* has started to invade the north of Tanzania. Both the global and particularly the regional model suggest that large parts of Tanzania are suitable habitat for *P. juliflora* and are therefore at a high risk of being invaded. Although none of our models contain occurrence points from southern Somalia, both models suggest that much of Somalia is a highly suitable region for *P. juliflora*. The

regional model additionally identifies large suitable areas in Sudan and South Sudan. However, it is important to note that modeling outputs for these three countries are less accurate due to missing presence data in our models.

Predictions for the future under changing climates suggest gains as well as losses of areas suitable for *P. juliflora* in the study countries as well as in neighboring regions. While the more extreme scenario (mp85) leads to greater areas at risk in Sudan and South Sudan compared to the more moderate scenario (mp45), it leads to smaller areas at risk in Tanzania. In Ethiopia and Kenya, gains and losses in suitable habitat are about the same and occur mostly along the borders of the areas predicted as currently suitable. To our knowledge, no other study so far has looked into how climate change will affect the habitat of *P. juliflora* at the global or regional scales. Accordingly, an evaluation of these findings is difficult.

In the case of *L. camara*, the Ethiopian and Kenyan highlands as well as northern and central Tanzania currently have the highest risk of being affected by *L. camara* invasion. This corresponds to findings from a global study by Qin et al. (2016) in which they predicted an expansion of *L. camara* further inland in Eastern Africa, particularly under the RCP85 emission scenario. The global model suggests that virtually all of Ethiopia and Kenya and most of Tanzania has suitable climates for *L. camara*, which likewise corresponds to the findings of Qin et al. (2016). However, this is not confirmed by the regional model, which we consider to be more accurate, as it uses local occurrence points and additional variables reflecting the preferred environmental conditions of the two species. Nonetheless, we would like to highlight areas in west central Tanzania where the Eastern African niche exceeds the global one and which might therefore have a higher risk of *L. camara* presence or invasion in the near future. This, too, is in line with findings reported by Qin et al. (2016). Our results further suggest that Zambia is at a high risk of being affected by *L. camara* in the future, although, again, we did not consider any occurrence data from Zambia and hence this finding might be less reliable. Considering future climatic changes, we observe small areas here and there where the risk of *L. camara* invasion increases or decreases. This corresponds to earlier findings reported by

Taylor et al. (2012), who characterized the likely future distribution of *L. camara* as patchy and determined by the existence of favorable microhabitats. Areas of increasing risk are mostly located in Tanzania, Somalia, and South Sudan, while areas of decreasing risk occur also in Tanzania, in Zambia, and in areas bordering the Ethiopian highlands.

Implications for effective invasive alien plant management

Both *P. juliflora* and *L. camara* have become widely established in Eastern Africa, necessitating a spatially explicit management strategy that ensures concerted communication and management across national and subnational borders and sets different control objectives for areas with different invasion levels (Grice et al. 2011, Terblanche et al. 2016, Shackleton et al. 2017b). By combining different approaches to assess the two species' ecological niches and stages of invasion and the probability of their potential distribution in space and time, our study generated a number of results with direct implications for management (Table 4).

Management of IAPS usually follows a three-stage hierarchical approach consisting of (1) prevention of establishment in areas where the IAPS is not yet present, (2) early detection and rapid response (EDRR) in areas where infestations are limited and accessible, and (3) control (Witt and Luke 2017). Prevention measures should primarily target areas that are climatically suitable, meaning areas that are within the ecological niche. In line with the young invasion history of *P. juliflora* in Eastern Africa, our results indicate that a regional or national spatially explicit management strategy for this species should emphasize prevention alongside EDRR and control. Our results indicate that large areas in Eastern Africa that have not yet been invaded by *P. juliflora* are suitable under the current climate or will become suitable under the predicted climate change scenarios. In an attempt to spatially delineate different regions in Australia necessitating different approaches to managing the invasive plant *Hymenachne amplexicaulis* (Rudge) Nees, Grice et al. (2011) distinguished between low- and high-risk prevention zones. Similarly, areas close to the invasion front in northern Tanzania should be declared as high-risk prevention

zones that require several prevention measures. For example, the spread of *Prosopis glandulosa* Torr. into non-infested areas in Western Australia was controlled by building large fences between invaded and non-invaded suitable areas, and by keeping livestock for several days in *Prosopis*-free paddocks before moving it into non-invaded areas (Van Klinken and Campbell 2009). Suitable areas in the central and southern parts of Tanzania could be considered as low-risk prevention zones, where it may be sufficient to emphasize prevention of *P. juliflora* planting as well as intentional and unintentional long-distance seed dispersal. Moreover, since our results suggest that new areas will become suitable in the context of climate change and, based on the analysis of the stage of invasion, *P. juliflora* may be able to adapt to novel climatic conditions, the planting of saplings and dispersal of seeds should also be prohibited in areas bordering the current range of suitable habitats (e.g., southwestern Tanzania and northern Zambia).

With regard to *L. camara*, which was introduced to Eastern Africa already in the 19th century (Day et al. 2003, Sharma et al. 2005), our results indicate that this species has already colonized a significant part of its ecological niche in Eastern Africa and that, therefore, prevention measures may be less warranted than in the case of *P. juliflora*. However, the global (i.e., using global occurrences without Eastern African occurrences) and Eastern African (i.e., using the Eastern African occurrences only) ensemble SDMs for Eastern Africa produced conflicting modeling outputs: Large areas in the lowlands of northern Kenya and Ethiopia are within the modeled global niche but not within the modeled Eastern African niche (Fig. 4). A possible explanation for these conflicting outputs is that the global niche, relative to the Eastern African niche, is based on a larger genetic variation of *L. camara*, with a higher variation in phenotypic traits that affect habitat suitability. Further studies are needed to accurately interpret these contradictory results and to decide whether regional or national *L. camara* management strategies in Eastern Africa should include prevention measures in lowland areas; for example, *L. camara* saplings could be experimentally transplanted across the areas that are included in the global but not in the Eastern African niche, and their

Table 5. Main findings of this paper and implications for IAPS management.

Findings	Management implications
<i>Assessment of ecological niches</i>	
The global and Eastern African niches of both <i>Prosopis juliflora</i> and <i>Lantana camara</i> overlap to a considerable extent	
The current Eastern African niche of <i>P. juliflora</i> largely contours the conditions in areas where <i>P. juliflora</i> was originally introduced	The high level of niche unfilling by <i>P. juliflora</i> at subnational level indicates that large areas not yet invaded are at risk of being invaded in the future
Niche unfilling varies considerably for <i>P. juliflora</i> when different “local” niches are compared	New plantations in suitable areas currently free of <i>P. juliflora</i> should be prohibited
Distance from waterbodies is an important variable in the Eastern African distribution model for <i>P. juliflora</i>	When searching for new <i>P. juliflora</i> infestations, particular emphasis should be placed on surveying waterbodies
<i>L. camara</i> appears to have colonized a significant part of its ecological niche in Eastern Africa	Management strategies for <i>L. camara</i> in Eastern Africa should primarily focus on keeping weed densities low and reducing high weed densities in the invaded range; prevention and EDRR appear to be less relevant, since the species is already widely distributed
<i>Climate change is expected to lead to small niche expansions for both species</i>	
Exclusion of marginal climates leads to considerable increases in percent niche unfilling for both species, but niche expansion remains low or zero	
<i>Stage of invasion</i>	
<i>P. juliflora</i> (1) is still spreading and (2) appears to be undergoing a relatively rapid local adaptation process	
The likelihood of adaptation to more marginal or even new climatic conditions is higher for <i>P. juliflora</i> than for <i>L. camara</i>	Prevention measures for <i>P. juliflora</i> should also be implemented in areas that are slightly outside the global ecological niche
<i>L. camara</i> appears to be close to reaching a quasi-equilibrium distribution in Eastern Africa	Management measures for <i>L. camara</i> can be restricted to areas within the global ecological niche
<i>Current potential suitable habitats</i>	
The global and the Eastern African habitat models for <i>P. juliflora</i> largely overlap, but the Eastern African model suggests that large areas in western Kenya and Tanzania also contain suitable habitats	A national <i>P. juliflora</i> strategy should be implemented in Tanzania to halt the recent invasion from Kenya
<i>P. juliflora</i> is likely to continue to spread in Tanzania	Awareness of the negative impacts of woody IAPS should be raised among the general public and other stakeholders in regions that are still uninvaded but contain suitable habitats for <i>P. juliflora</i> (and to a lesser extent also <i>L. camara</i>)
The Ethiopian and Kenyan highlands are severely affected or at high risk of being invaded by <i>L. camara</i>	National authorities should coordinate IAPS management in border regions to prevent invasion of new countries or areas
There are large areas in Eastern Africa where the global and the Eastern African models for <i>L. camara</i> do not overlap	The significant differences in the geographic representation of suitable habitats for <i>L. camara</i> between the global and the Eastern African models entail uncertainty about whether lowland regions in Ethiopia and Kenya need to be surveyed for new infestations
<i>Future potential suitable habitats</i>	
Invasion of <i>P. juliflora</i> in Tanzania is likely to accentuate under future climates	<i>P. juliflora</i> surveillance programs should include habitats that will become suitable with climate change (particularly southwestern Tanzania)
In the context of a changing climate, regions outside the study region (e.g., Zambia) are at risk of being invaded by <i>P. juliflora</i>	Planting of <i>P. juliflora</i> and the intentional introduction of seeds (e.g., by livestock crossing the borders) to northern Zambia (e.g., from Tanzania) should be prohibited
	Early detection of <i>P. juliflora</i> and rapid response near the invasion front in northern Tanzania should be prioritized
Climate change appears to have little impact on the availability of suitable habitats for <i>L. camara</i> in the study region, except for a decrease in suitable habitats in central Tanzania	

Note: EDRR, early detection and rapid response.

performance measured (Angert and Schemske 2005).

Early detection and rapid response and control measures will be important additional elements of regional and national management strategies against both target weeds. However, spatial targeting of EDRR and control measures requires detailed maps of the two species' current distribution, ideally with information on local abundance or cover (Table 5; Frazier and Wang 2011, Shiferaw et al. 2019).

CONCLUSION

Our study suggests that the combination of different approaches in niche shift studies of IAPS can provide significant insight into current and projected future IAPS invasion processes, but it can also generate conflicting results or even suggest an overestimation of niche filling. The comparative assessment of the ecological niches, stages of invasion, and potential distribution of *P. juliflora* and *L. camara* in Eastern Africa revealed patterns that largely reflect the different invasion histories of the two species. Importantly, the combination of approaches enabled us to formulate general and specific recommendations with regard to prevention measures—an important component of IAPS management strategies. To inform the other key components of IAPS strategies, EDRR and control, niche shift studies should be combined with other approaches, such as fractional cover maps of the current distribution of IAPS (Frazier and Wang 2011).

As emphasized by Guisan et al. (2014), correlative niche shift studies of exotic species may also guide experimental studies, but a combined approach has rarely been applied so far (Hill et al. 2013). Experimental studies addressing the conflicting results generated by the different approaches—such as the large differences in the suitable geographic areas predicted by the global and the Eastern Africa models for *L. camara*—would be particularly useful for further improving spatially explicit IAPS management strategies at the national or regional level.

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